

## TERRESTRIAL HYDROMETRIDAE (HETEROPTERA) FROM MADAGASCAR, AND THE REMARKABLE THORACIC POLYMORPHISM OF A CLOSELY RELATED SPECIES FROM SOUTHEAST ASIA

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*Abstract.*—Two new species of terrestrial *Hydrometra*, *H. phytophila* and *H. cavernicola*, are described from the rain forests of Mt. d'Ambre in northern Madagascar. The first species occurs in understory vegetation, often far from streams, and the second on damp rock walls; these are the first truly terrestrial Hydrometridae reported. These new taxa belong to a monophyletic subgroup within *Hydrometra* whose other members occur in Madagascar, Ceylon, and southeast Asia, a vicariant distribution pattern which is interpreted to have arisen via the rifting of Madagascar from India in the Cretaceous. One Asian member of this complex, *H. aberrans* Hungerford and Matsuda, is found to exhibit a remarkable polymorphism in regard to the presence or absence of a large tubercle on the thoracic dorsum. Aptery within the genus *Hydrometra* is discussed in comparison to other members of the Gerromorpha. A check list of *Hydrometra* species occurring in Madagascar is provided.

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Members of the family Hydrometridae have been traditionally considered as semiaquatic insects whose existence is closely tied to aquatic habitats. It was thus with some surprise that the junior author discovered one in his net far from any stream while sweeping for terrestrial Heteroptera in the understory vegetation of the Mt. d'Ambre forest reserve in northern Madagascar. His suggestion that this specimen might have come off plants was met with general skepticism by others in the collecting party, who proposed instead that it must have been carried in the net from a previous stream locality. A similar discovery by the same author at a different site the following day, however, led to an intensive search that proved nymphs and adults of this insect do indeed inhabit vegetation, even at considerable distances from water, a habit quite different from that previously documented for any other *Hydrometra* species.

A closely related new species was also found on the same mountain inhabiting damp rock walls in caves and dark rock-holes in waterfall splash zones. This second species apparently is restricted to hygroscopic habitats, and was never found on the surfaces of adjacent streams. The presence of this closely allied species with an annectant behavior pattern and habitat preference strongly suggests that the transition from a subaquatic to terrestrial existence in *Hydrometra* has occurred locally in the rain forests of Madagascar, and that this ecological character can be useful in assessing phylogenetic relationships. In addition to the two unusual species noted above, several *Hydrometra* species with typical morphology and behavior (*H. fanjahira* Hungerford and Evans, *H. bifurcata* Hungerford and Evans) were also abundant on the streams of Mt. d'Ambre, so that at this single locality the entire spectrum of ecological roles in the genus, from semiaquatic to terrestrial, was represented.

Although the new species described herein is the first truly terrestrial hydrometrid

documented, various taxa within the family are known to spend portions of their lives on land. Temperate zone species of *Hydrometra* frequently retreat to moist streamside habitats of leaf litter and damp moss in winter to avoid the ice that forms on their aquatic habitats (Hungerford, 1920; Andersen, 1982). *Chaetometra robusta* was collected from ferns in the Marquesas Islands (Hungerford, 1939), and the type locality of *Heterocleptes hoberlandti* was listed as "detritus on soil" in the gallery forest along the Luachino River in Angola. In all of the above cases, though, these species were found very near water in riparian habitats.

The two new species from northern Madagascar are most closely allied to *H. madagascarensis* Hungerford and Evans, known from the eastern rain forests of the island. Outside Madagascar the closest relatives of these three species are *H. zeylanica* Gunawardane and Karunaratne from Ceylon, and *H. longicapitis* Bueno and *H. aberrans* Hungerford and Matsuda from southeast Asia. The distinctively narrow elongated head and relatively short thorax shared by all these taxa are not found in any known African species, despite the close geographical proximity of Madagascar to that continent. The present distribution and relationships argue instead for a vicariance pattern involving India and Madagascar, probably dating from the rifting of Gondwanaland in the Cretaceous. A similar distribution pattern is seen in Lepidoptera, ptilomerine Gerridae, and certain mayflies, and we hypothesize that India and Madagascar were separated from Africa as an intact subcontinent, with India subsequently rifting from Madagascar and drifting north across the equator to contact southern Asia. Many elements of the tropical fauna carried on India were then able to disperse into the ancient rain forests of southeast Asia via Assam and Burma. The continuing rise of the Himalaya in response to the impact of drifting India has caused desertification of the central Indian subcontinent, leaving Ceylon as an isolated tropical refugium and producing the discontinuous distributions seen today.

All measurements are given in millimeters. Specimen depository abbreviations are indicated in the acknowledgments. This research was supported in part by a grant from the National Geographic Society, Washington, D.C.

### ***Hydrometra phytophila*, new species**

Figs. 1-4, 8, 9

*Diagnosis.* *Hydrometra phytophila* is very closely related to *Hydrometra madagascarensis* Hungerford and Evans (1934). It differs from the latter in having the lateral spines on the base of abdominal sternite VII closer to the medial spines, the anteocular part of the head much shorter in relation to the postocular part (ratio AO/PO for *phytophila* = 2.01, for *madagascarensis* = 2.65), and the connexiva light except narrowly on the margins (versus broadly black).

*Description.* Extremely long and slender; only apterous and micropterous forms known. Ground color yellow brown; abdominal tergites shining, lighter. Head, thorax lightly frosted. Venter mostly yellowish; collar, coxal cavities slightly darker. Connexiva narrowly margined with black, also narrowly along abdominal tergites in female. Legs, antennae brownish yellow; antennal segments I-II distally, distal  $\frac{1}{10}$  of III-IV, all tibia distally, rostrum distally, ventral lobe of head, brownish; all femora contrasting deep brown on distal  $\frac{1}{10}$ .

Structural characteristics: Head extremely long (4.29 mm), widest (0.35 mm) at

antennal tubercles; ventral lobe large (Fig. 1); rostrum reaching behind eyes; ratio anteocular/postocular portions: 2.73/1.36 mm; interocular space/width of an eye: 0.11/0.14 mm; clypeus narrow, forming an acute angle apically, tip narrowly rounded. Antennal formula I–IV: 0.40; 1.16; 4.80; 1.82 mm. Prothorax with an encircling row of pits anteriorly, demarcating collar; anterior pronotal lobe with tiny pits usually marked with white; posterior lobe with numerous small deep pits. Pronotum length 1.21 mm; remainder of thorax 1.16 mm; abdomen length 5.30 mm. Distance between anterior and middle coxae (measured between closest margins) 0.45 mm; between middle and hind coxae 1.10 mm. Anterior coxae with 2 pits on anterior part, 2 on posterior part; middle coxae with 2 pits on anterior part, 3 on posterior part; hind coxae with 2 pits.

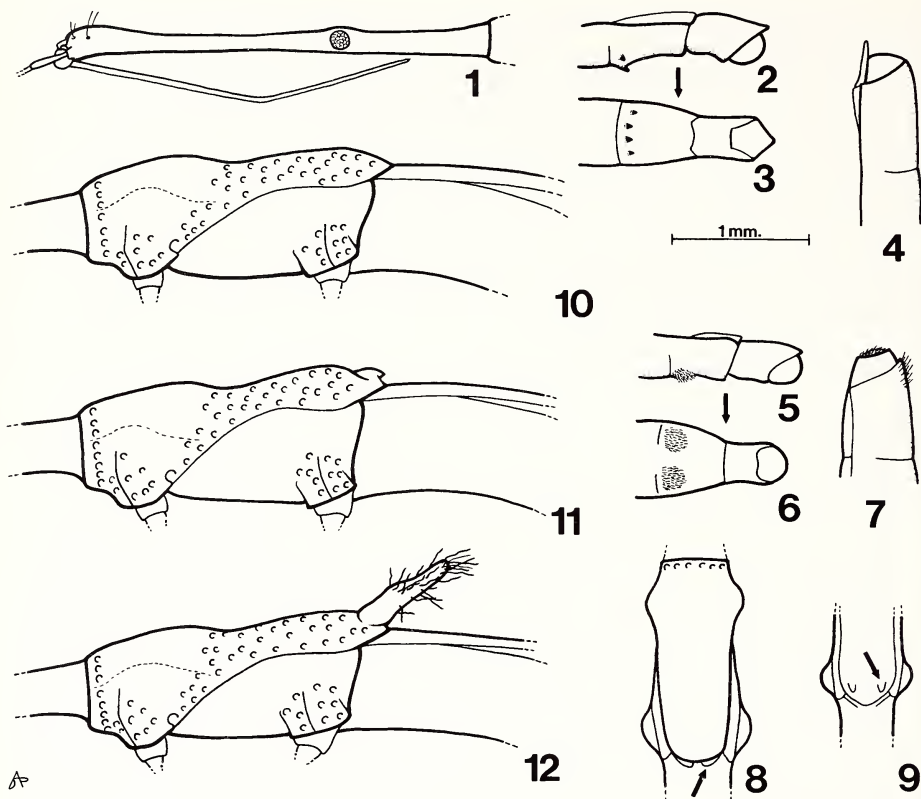
Proportions of legs as follows, in mm:

	Femur	Tibia	Tarsal 1	Tarsal 2	Tarsal 3
Anterior	3.94	5.25	0.10	0.35	0.20
Middle	4.19	5.56	0.10	0.30	0.15
Posterior	5.86	8.94	0.10	0.35	0.15

Male and female with abdominal terminalia and genital segments as shown in Figures 2–4. Length, apterous male 12.38 mm; apterous female 12.58 mm.

*Discussion.* *Hydrometra phytophila* is a member of a monophyletic subgroup within *Hydrometra* that also contains *H. cavernicola* n. sp. and *H. madagascarensis* Hungerford and Evans. The closest apparent relatives of these species are *Hydrometra zeylanica* Gunawardane and Karunaratne from Ceylon and *H. longicapitis* Bueno and *H. aberrans* Hungerford and Matsuda from southeast Asia. The latter share with all three of the above species the following characteristics: very long slender body; relatively short thorax; both head and abdomen elongated and conspicuously longer than the thorax; head with small maxillary plates and large ventral lobes; male abdominal segment VII short, shallowly excavate medially with ventral processes near anterior margin; male genital segments not modified (terminology follows Andersen, 1982). The Asian members of this group differ from the Malagasy species in the following respects: the clypeus is somewhat broader; in the female of both species and the male of the latter the abdomen is curved; the apterous forms are unknown. A review of the *Hydrometra* species of the world reveals that while a Neotropical group (including *H. caraiba* Guérin-Meneville, *H. huallagana* Drake, *H. olallai* Mychajliw and *H. metator* White) plus *H. papuana* Kirkaldy from the Malay Archipelago all share with the above species the very long head, it is not nearly as slender, and the thorax is elongated and subequal in length to both the head and abdomen.

The three Madagascar species discussed here are all apterous except for one micropterous female (Fig. 8), seemingly an apomorphy for this group. The significance or even the definition of aptery in *Hydrometra* is, however, unclear. The phenomenon seems to be quite rare in the genus, and further it is not certain that true aptery even occurs. Torre-Bueno (1926) stated that of the many *Hydrometra martini* Kirkaldy that he studied a few were apterous, however we are unable to confirm the existence of this morph in *martini*; we have examined many specimens, and those that appeared apterous in dorsal view have tiny wing pads hidden under the posterior margin of the pronotum, visible without dissection. Almost all species of *Hydrometra* are rep-



Figs. 1-4, 8, 9. *Hydrometra phytophila*. 1. Head. 2. Male abdomen, lateral view. 3. Male abdomen, ventral view. 4. Female abdomen, lateral view. 8. Thorax, micropterous form, dorsal view, showing small wing pads (arrow). 9. Thorax, apterous form, dorsal view with pronotal lobe removed, showing wing rudiments (arrow).

Figs. 5-7. *Hydrometra cavernicola*. 5. Male abdomen, lateral view. 6. Male abdomen, ventral view. 7. Female abdomen, lateral view.

Figs. 10-12. *Hydrometra aberrans*, thorax, lateral view, showing three pronotal morphs. 10. Normal form. 11. Pronotal lobe with incipient tubercle. 12. Pronotal lobe with tubercle, the *aberrans* form.

resented in the Polhemus collection and a quick survey revealed only two species that are predominately wingless and seem to be potentially apterous, aside from the three Madagascar taxa discussed above: *Hydrometra hungerfordi* Bueno and *Hydrometra aculeata* Montrousier. When the pronotum of each of these species is removed, small strap-like wings are revealed that do not reach the posterior pronotal margin; these are not visible without dissection. The reduction in *H. phytophila* n. sp. and *H. cavernicola* n. sp. is even more profound, as the wings are represented by tiny fleshy buds far removed from the posterior margin of the pronotum (Fig. 9), visible only after removal of the pronotal lobe. This apparently does not represent true aptery in the same sense as in Gerromorphan genera where the thoracic sclerites of the truly apterous morph are dramatically different from those of the winged morph



and there are clearly no wing rudiments, e.g., *Mesovelvia*, *Limnogonus*, *Eurygerris*, *Gerris* (the two different forms of aptery in *Gerris* were illustrated and discussed by Andersen, 1982, pp. 296–301). We predict that if and when a *Hydrometra* species is found without wing rudiments it will have a much altered thoracic morphology.

The very long narrow head coupled with a shortened thorax and predominant flightlessness are considered to be derived states, the latter perhaps a consequence of the return to a terrestrial habitat.

*Habitat data.* The forest at the Mt. d'Ambre type locality is a primary moist montane forest which was selectively logged for valuable hardwoods during the French colonial period but has subsequently been left undisturbed and allowed to regain its original stature. Dominant tree species are members of the Sapindaceae, Sapotaceae and Myrtaceae which form a closed canopy approximately 25 m above the ground. The type series of *Hydrometra phytophila*, n. sp. was taken by sweeping the understory vegetation below this canopy. The insects were especially abundant on ferns and soft stemmed vegetation, however JTP found several specimens on earth beneath the vegetation on a trailside bank. Individuals were frequently taken at great distances (up to several km) from any discernable water source, and in collecting along transects perpendicular to the stream near Petite Cascade they were not found closer than 1 meter to the stream, indicating that they are truly terrestrial in habit and not closely tied to riparian communities.

*Etymology.* The name *phytophila* refers to the preferred microhabitat of this species, on shaded forest vegetation.

*Holotype apterous male and allotype apterous female.* MADAGASCAR, Diego Suarez Province, Petite Cascade trail, Montagne d'Ambre Forest Reserve, south of Diego Suarez, 990 m (3,250 ft), 16 November 1986, CL 2280, J. T. & D. A. Polhemus (USNM).

*Paratypes.* MADAGASCAR, Diego Suarez Province. Many apterous males and females, 1 micropterous female, same data as holotype (JTPC; TSIM); 1 apterous male, 1 apterous female, Grande Cascade, ragged rock face beside waterfall, Montagne d'Ambre forest reserve, 670 m (2,200 ft), 14 November 1986, CL 2278, J. T. & D. A. Polhemus (JTPC).

### ***Hydrometra cavernicola*, new species**

Figs. 5–7

*Diagnosis.* *Hydrometra cavernicola* is most closely related to *H. madagascarensis* Hungerford and Evans and *H. phytophila*; see discussion under the latter above. *H. cavernicola* may be separated from *H. madagascarensis* by the much shorter anteocular portion of the head (ratio AO/PO for *cavernicola* = 2.08, for *madagascarensis* = 2.65), and from *H. phytophila* by the medially dark abdominal tergites which are weakly carinate on their midline, versus non-carinate light tergites in *phytophila*, and by the brush-like processes on sternite VII versus dark acuminate structures in the latter species.

*Description.* Long and slender; only apterous form known. Ground color light brown; abdominal tergites not shining, lighter laterally, tergites II–VI carinate and brown medially. Venter mostly yellowish; collar, coxal cavities slightly darker. Connexiva narrowly margined with blackish brown shading to yellowish medially, brown along abdominal tergites except broadly yellowish behind segmental sutures. Legs, antennae brown; all femora contrasting deep brown on distal  $\frac{1}{20}$ .

Structural characteristics: Head very long (4.14 mm), widest (0.40 mm) at antennal tubercles; ventral lobe large; rostrum reaching behind eyes; ratio anteocular/post-ocular portions: 2.68/1.32 mm; interocular space/width of an eye: 0.11/0.18 mm; clypeus narrow, tapering anteriorly, tip broadly rounded. Antennal formula I–IV: 0.51; 1.16; 5.15; 2.07 mm. Prothorax with an encircling row of pits anteriorly, demarcating collar; anterior pronotal lobe and to a lesser degree posterior lobe with tiny pits usually marked with white; posterior lobe with numerous small deep pits. Pronotum length 1.33 mm; remainder of thorax 1.44 mm; abdomen length 5.15 mm. Distance between anterior and middle coxae (measured between closest margins) 0.54 mm; between middle and hind coxae 1.30 mm. Anterior coxae with 2 pits on anterior part, 2 on posterior part; middle coxae with 2 pits on anterior part, 3 on posterior part; hind coxae with 3 pits.

Proportions of legs as follows, in mm:

	Femur	Tibia	Tarsal 1	Tarsal 2	Tarsal 3
Anterior	4.46	4.85	0.07	0.25	0.25
Middle	4.86	5.30	0.07	0.22	0.10
Posterior	6.19	8.43	0.07	0.18	0.25

Male and female with abdominal terminalia and genital segments as shown in Figures 5–7. Length, apterous male 12.00 mm; apterous female 12.80 mm.

*Discussion.* The relationship of this species to other *Hydrometra* species is discussed above under *H. phytophila*.

*Habitat data.* The type series of *H. cavernicola* was taken from the damp rock walls of a basalt cave adjacent to the Petite Cascade at Mt. d'Ambre, in company with emesine Reduviidae. The insects were slow or inactive until disturbed, but would then move quickly across the vertical rock surface in attempts to escape. At the Grand Cascade locality specimens were taken from dark pockets protected by overhanging rock on the rugged basalt wall next to the waterfall.

*Etymology.* The name *cavernicola* refers to the preferred microhabitat of this species, in moist, shaded caverns and rock holes.

*Holotype apterous male and allotype apterous female.* MADAGASCAR, Diego Suarez Province, Petite Cascade, cave alongside plunge pool, Montagne d'Ambre Forest Reserve, south of Diego Suarez, 990 m (3,250 ft), 16 November 1986, CL 2280, J. T. & D. A. Polhemus (USNM).

*Paratypes.* MADAGASCAR. Diego Suarez Province. Many apterous specimens, males and females, same data as holotype (JTPC, TSIM); 2 apterous males, 1 apterous female, Grande Cascade, ragged rock face beside waterfall, Montagne d'Ambre forest reserve, 670 m (2,200 ft), 14 November 1986, CL 2278, J. T. & D. A. Polhemus (JTPC).

#### *Hydrometra madagascarensis* Hungerford and Evans

*Hydrometra madagascarensis* Hungerford, H. B. and N. E. Evans, 1934. Ann. Mus. Nat. Hung. 28:87 (Described from 1 male and 1 female, Foret Tanala, Reg. de Ranomafana).

*Discussion.* We have examined specimens from a long series of this species housed in the Zoological Institute of Leningrad. Although we collected in aquatic habitats near Perinet, where the Leningrad series originated, we did not encounter this species.

The type data for *H. madagascarensis* state that it was collected in the Tanala Forest, and this data plus the close relationship to the terrestrial species taken later in our expedition suggest that *H. madagascarensis* may also be terrestrial.

*Material examined.* MADAGASCAR, Tamatave Province, 4 apterous males, 2 apterous females, Perinet, XII-1932 (JTPC; exchange from Zoological Institute, Leningrad).

#### CHECKLIST OF *HYDROMETRA* SPECIES OCCURRING IN MADAGASCAR

All of the species below are endemic to Madagascar with the exceptions of *H. carayoni* Poisson, described from the Camaroons, and *H. albolineolata* Reuter, a species widely distributed in Africa. We have not been able to confirm the presence of *H. albolineolata* in Madagascar, even though we made collections on the Ankaratra Range in the vicinity of Manjakatempo, a locality from which this species was previously reported (Poisson, 1948). Our determination of *carayoni* is uncertain because we have not been able to examine the type of this species.

<i>Species</i>	<i>Distribution in Madagascar</i>
<i>H. albolineolata</i> Reuter 1882	Manjakatempo (Ankaratra)
<i>H. bifurcata</i> Hungerford and Evans 1934	Widespread
<i>H. carayoni</i> (?) Poisson 1948	Perinet
<i>H. cavernicola</i> J. and D. Polhemus n.sp.	Mt. d'Ambre
<i>H. fanjahira</i> Hungerford and Evans 1934	Widespread
<i>H. isaka</i> Hungerford and Evans 1934	Widespread
<i>H. madagascarensis</i> Hungerford and Evans 1934	Eastern rain forest region
<i>H. phytophila</i> J. and D. Polhemus n. sp.	Mt. d'Ambre

#### *Hydrometra aberrans* Hungerford and Matsuda Figs. 10-12

*Hydrometra aberrans* Hungerford, H. S. and R. Matsuda, 1961. J. Kansas Entomol. Soc. 34:62 (unique female type from Selangor, Malaysia).

*Discussion.* Years ago one of us (JTP) studied a small series of *Hydrometra* from Thailand in the California Academy of Sciences that contained both typical *H. aberrans*, with its distinctive thoracic tubercle in the females, and examples of another quite similar but atuberculate "species." At the time it was hypothesized that the females might be polymorphic forms of a single species, because a detailed examination of every characteristic that could possibly separate them revealed only the bizarre pronotal tubercle of the *aberrans* form, and only a single male form was present. This hypothesis was confirmed when we very fortunately obtained a good series of both morphs plus an intermediate form from a single population in the swamp forests of Johor, peninsular Malaysia.

A careful examination of the females reveals that in addition to the "normal" atuberculate female and the bizarre *aberrans* form there is yet another morph that has a small "button," appearing as an incipient tubercle in the same location on the pronotum as the long process of the *aberrans* form (Figs. 10-12). We have found this form in the Johor series, and in another female from Thailand. As far as we know, this remarkable polymorphism is without parallel in the aquatic Heteroptera.



We have had great difficulty in distinguishing the atuberculate morphs of *H. aberrans* from individuals of the closely allied *H. longicapitis* Bueno, which occurs sympatrically over much of the same geographical range. Our initial inclination was to consider the two species synonymous, but N. M. Andersen (pers. comm.) has stated that he believes these species are distinct, and that there are in fact other undescribed species from Indochina in this same tightly allied complex. Hungerford and Matsuda (1961) discussed the separation of *H. longicapitis* and *H. aberrans*, citing four points of difference. Setting aside 1, the conspicuous caudal pronotal projection of the *aberrans* form, these are discussed in turn for females only, the males being monotonous in all series we have seen and not exhibiting any discernable polymorphisms.

2. Body size: The body of *H. aberrans* (from Malaysia) was said to be larger than that of *H. longicapitis* (from Thailand). We have a small female from Chiang Mai, Thailand but we also have females of equal size for both forms from other series taken in both Thailand (Khao Yai Nat. Pk.) and Malaysia (Johor); most specimens are of similar size regardless of locality.

3. Contour of the abdomen: The type of *H. aberrans* has the abdomen curved upward, rising to the distal margin of tergite V (fourth visible), then bent so that tergites VI and VII are horizontal (see fig. 4 in Hungerford and Matsuda, 1961). The abdomen of *H. longicapitis* was said to be curved over all of its length. All of our "*aberrans*" females are the same as *H. longicapitis* in this regard, except for one female with an incipient pronotal tubercle from Malaysia in which the abdomen is not entirely curved but is instead the same as shown for the type of *H. aberrans*. This appears to constitute yet another polymorphism in the females of this species.

4. Width of the abdominal tergites: These were said to be broader in *H. aberrans*, but we find this character to be variable in the series at hand, and the two forms are clearly not separable on this basis.

The characters previously used to define these species are thus rather weak and variable. Presumably Andersen's future investigations will produce less ambiguous species concepts based on a more thorough character analysis.

We have reviewed a file of correspondence between Dr. C. H. Fernando, Mr. P. B. Karunaratne and Prof. H. B. Hungerford, sent for study by Dr. K. V. Krombein along with the associated Karunaratne collection of Malaysian Hydrometridae (USNM). In a 1963 letter Hungerford stated that he had received from Fernando two macropterous females of *H. aberrans*, one with the pronotum like the type, the other with the pronotum normal! Thus within two years after the original description Hungerford recognized that polymorphism existed in this species, but apparently neither he nor any of the other workers involved ever published this discovery.

*Habitat data.* We found *H. aberrans* to be abundant along the margins of smoothly flowing swamp forest streams in the lowlands of southern Malaysia. The insects seemed to frequent small bars of mud or damp sand at the water's edge, and were usually detected when they ran out onto the water at our approach. If pursued they would leave the water and run back up onto the muddy banks, attempting to gain shelter amid roots and streamside vegetation.

*Material examined.* (All in JTPC, and all of the normal atuberculate form unless otherwise noted.) THAILAND. *Chiang Mai Province.* 1 macropterous male, Mae Sa, 16 km NW Chiang Mai, base of Mt. Doi Sutep, XII-23-1981, A. R. Gillogly; 1 macropterous male, 1 micropterous female, Chiang Mai, Lot No. 275, III-1-1962,



D. C. & E. B. Thurman. *Parjinburi Province*. 1 brachypterous female, Kabinburi, XII-2 to 5-1965, Koi Mongkolpanya. *Province uncertain*. 1 macropterous male, 1 macropterous female (*aberrans* form), 2 brachypterous females (1 *aberrans* form; 1 "incipient tubercle" form), Khao-Yai Nat. Pk., 750 m, VII-26-1962, E. S. Ross, D. Q. Cavagnaro (JTPC, CAS). INDONESIA. *Sumatra Utara Province*. 1 brachypterous female, Dolok Merangir, E. W. Diehl. MALAYSIA. *Johor*. 11 brachypterous males, 7 brachypterous females (2 *aberrans* form, 2 "incipient tubercle" form), swamp forest stream, 61 km NE of Johor Bharu on Mersing Road, CL 2220, X-16-1986, J. T. & D. A. Polhemus; 14 brachypterous males, 2 brachypterous females (1 "incipient tubercle" form), swamp forest stream, 25 km W of Sedili Besar, 20 m, CL 2218, X-16-1986, J. T. & D. A. Polhemus; 2 brachypterous males, 1 brachypterous female, Sungai Wan Tenga, XI-1-1968, J. I. Furtado (USNM, Karunaratne Collection). *Selangor*. 6 brachypterous females (all *aberrans* form), Sungai Klang, Klang Gate, I-14-1962, J. I. Furtado (USNM, Karunaratne Collection).

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